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New Crested Pterosaurs from the Lower Cretaceous of Brazil

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With 4 Figures

Abstract

A complete skull and a mandible of large pterosaurs from the Aptian Santana Formation of the Chapada do Araripe in northeastern Brazil are described and assigned to a new genus, *Tropeognathus* nov. gen., including two new species, *Tr. mesembrinus* nov. sp., and *Tr. robustus* nov. sp.. The new genus is characterized by the development of high, sagittal, bony crests at the front end of the premaxilla and the symphysis of the mandible. The function of these terminal crests is interpreted as being hydrodynamic stabilizers of the jaws skimming the water while catching fish. A possible relationship of these forms to the Criorhynchidae of the English Cretaceous is discussed.

Kurzfassung

Aus der Santana-Formation (Apt) der Chapada do Araripe in Nordost-Brasilien werden ein Schädel mit Unterkiefer und ein zweiter Unterkiefer beschrieben und einer neuen Flugsaurier-gattung, *Tropeognathus* nov. gen., mit zwei Arten, *Tr. mesembrinus* und *Tr. robustus*, zugeordnet. Es handelt sich um sehr große Formen mit hohen sagittalen Knochenkämmen am Schnauzenende, deren Funktion als hydrodynamische Stabilisatoren beim Fischfang gedeutet wird. Eine mögliche Verwandtschaft mit den Criorhynchidae der englischen Kreide wird diskutiert.

Introduction

During recent years the Santana Formation (Aptian) fossil localities of the Chapada do Araripe in the provinces Ceará and Pernambuco in northeastern Brazil have produced an increasing number of pterosaurian remains. Since Price (1971) described the first pterosaur, *Araripesaurus castilhoi*, up to now five more genera including nine different species have been established. Only four of these are known by skull material: *Cearadactylus atrox* Leonardi & Borgomanero 1985, *Araripesaurus santanae* Wellnhofer1985, *Santanadactylus araripensis* Wellnhofer 1985, and *Anhanguera blittersdorffi* Campos & Kellner 1985.

Brasileodactylus araripensis Kellner 1984 was based on a symphysis of a mandible.

Only in *Araripesaurus santanae* and *Santanadactylus araripensis* cranial material is associated with wing elements, whereas the remaining five species are based on postcranial elements,

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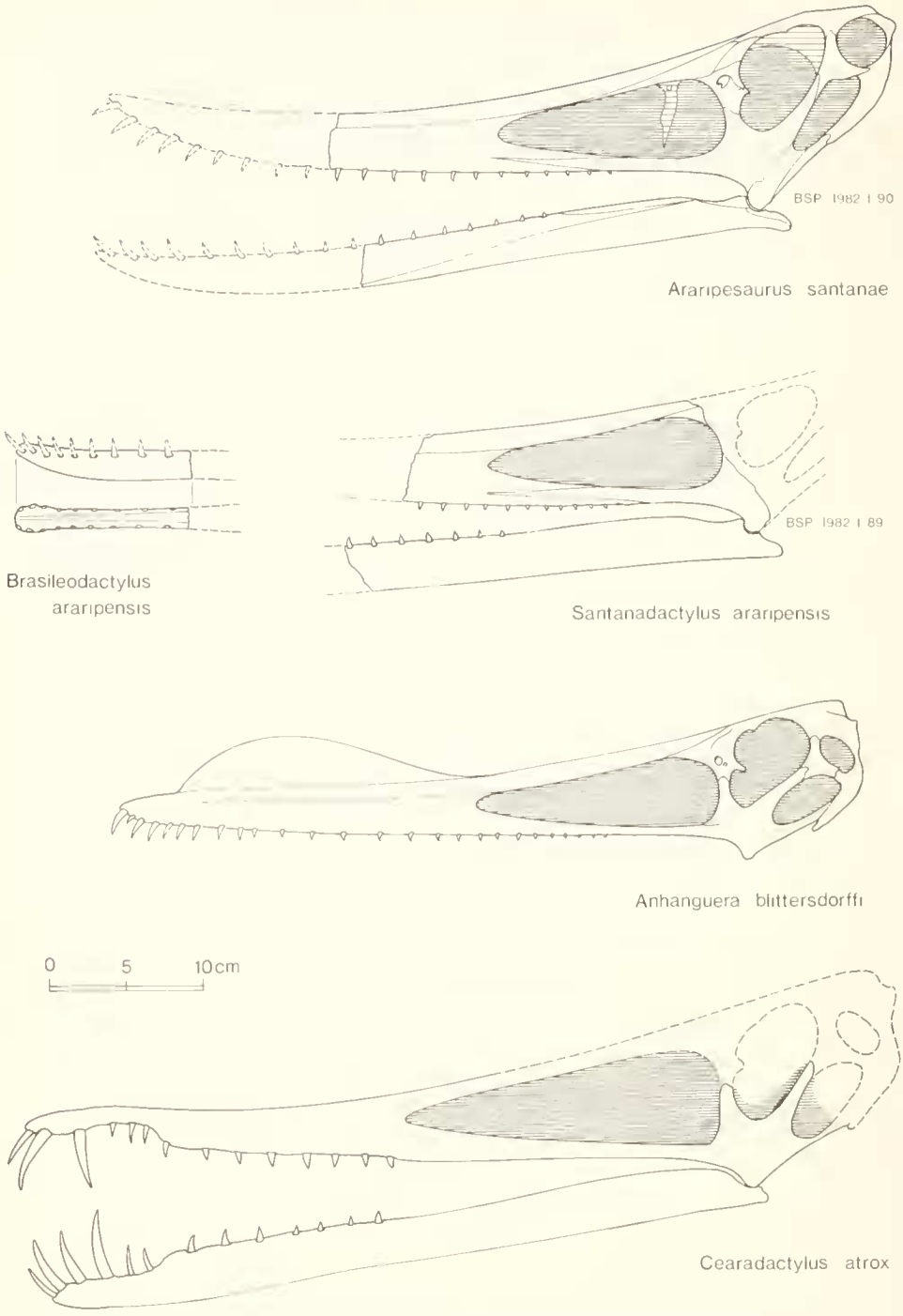


Fig. 1: Skulls of Santana pterosaurs hitherto described. Redrawn to the same scale after CAMPOS & KELLNER (1985), KELLNER (1984), LEONARDI & BORGOMANERO (1985), and WELLNHOFER (1985).

mostly wing bones and vertebrae. These are: *Araripesaurus castilhoi* Price 1971, *Araripedactylus dehmi* Wellnhofer 1977, *Santanadactylus brasilensis* De Buisonje 1980, *Santanadactylus pricei* Wellnhofer 1985, and *Santanadactylus spixi* Wellnhofer 1985.

Table 1 summarizes the type material on which the ten species of Santana pterosaurs have been based:

Araripesaurus castilhoi Price 1971

- radius
- ulna
- carpals
- metacarpals
- phalanges

Araripesaurus santanae Wellnhofer 1985

- skull
- mandible
- ulna
- radius
- carpals
- metacarpal

Araripedactylus dehmi Wellnhofer 1977

- first wing phalanx

Santanadactylus brasilensis De Buisonje 1980

- humerus, proximal end

Santanadactylus araripensis Wellnhofer 1985

- skull
- mandible
- humerus
- ulna
- radius
- carpus
- metacarpals

Santanadactylus pricei Wellnhofer 1985

- ulna
- radius
- carpals
- metacarpals
- pteroid
- first wing phalanx

Santanadactylus spixi Wellnhofer 1985

- ulna
- radius
- carpals
- pteroid
- metacarpal IV

Cearadactylus atrox Leonardi & Borgomanero 1985

skull
mandible

Anhanguera blittersdorffi Campos & Kellner 1985

skull

Brasileodactylus araripensis Kellner 1984

mandible, distal end

In the present state of our knowledge we do not know whether the isolated skulls of *Cearadactylus* and *Anhanguera* or the partial mandible of *Brasileodactylus* can be correlated with some of the postcranials hitherto assigned to other taxa. It may well be that the study of more complete material will result in a reduction of taxonomic units in the future. At the moment, this is not possible, however. New material presently being studied and in part presented here suggests even more new forms, indicating a high degree of pterosaur diversity in the Araripe region during Aptian times.

So, the Santana Formation of the Chapada do Araripe, originally famous for its fossil fishes, has become increasingly one of the most important pterosaur localities of the world, both with regard to the number and diversity of specimens and species and the perfect state of preservation, since the skeletal elements enclosed in nodules are usually uncrushed and hardly compressed. If thorough and skilled preparation is applied, most bones can be prepared out of the matrix completely.

In this paper two new forms of Santana pterosaurs, housed in the Bayerische Staatssammlung für Paläontologie und historische Geologie in Munich, are described: specimen BSP 1987 I 46, skull and mandible, and specimen BSP 1987 I 47, a mandible. The exact localities are not known and can only be given as "Chapada do Araripe", a vast plateau on the border between the states of Ceará and Pernambuco in northeastern Brazil. Fossilferous localities are known all around this plateau (see Campos & Wenz 1982). The geological and stratigraphical situation of the Santana Formation has been discussed elsewhere (see Wellnhofer, Buffetaut & Gigase 1983, Wellnhofer 1985, Maisey 1986, and others).

Systematic Description

Suborder PTERODACTYLOIDEA Plieninger 1901
Family ?Criorhynchidae Hooley 1914
Genus *Tropeognathus* nov. gen.

Type species: *Tropeognathus mesembrinus* nov. gen., nov. sp.

Etymology: trópis (Greek) = keel, gnáthos (Greek) = jaw. Named for the keeled jaws.

Diagnosis: Large pterodactyloid pterosaurs with premaxillary and mandibular sagittal crests at the front end of the skull and mandible. Strong, curved teeth from the tip of the jaws back to at least half the length of the jaws, decreasing in size.

Tropeognathus mesembrinus nov. gen., nov. sp.
Fig. 2

Holotype: BSP 1987 I 46, Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich, Skull and lower jaw.

Horizon and locality: Santana Formation, Lower Cretaceous, Aptian, Chapada do Araripe, probably province of Ceará, northeastern Brazil.

Etymology: mesembrinós (Greek) = southern. Named for the occurrence in the southern hemisphere.

Diagnosis: *Tropeognathus* with high, rounded sagittal crest on top of the premaxilla, and similar but smaller mandibular crest on the symphysis. Short and blunt parietal crest overhanging the occiput. High, medial ridge on the palate corresponding to a deep groove on the mandibular symphysis. Upper and lower jaws are not expanded anteriorly. Dentition with 13 premaxillary and maxillary teeth and 11 mandibular teeth in each side.

Skull: Originally, skull and mandible were preserved in one concretion, but could be separated. The skull is complete, except for most of the teeth. The premaxillary forming the bony bar as roof above the nasopreorbital fenestra has been depressed, and the tip of the snout is slightly bent to the left. Otherwise no bones are displaced. Preparation was carried out by mechanical tools including abrasive only. The skull openings were freed from the matrix as far as was necessary to show their margins. On the left side the orbit and the two temporal fenestrae were excavated for the most part to their bony bases, the inner wall of the braincase, leaving a free standing framework composed of the postorbital, squamosal, jugal, and quadrate.

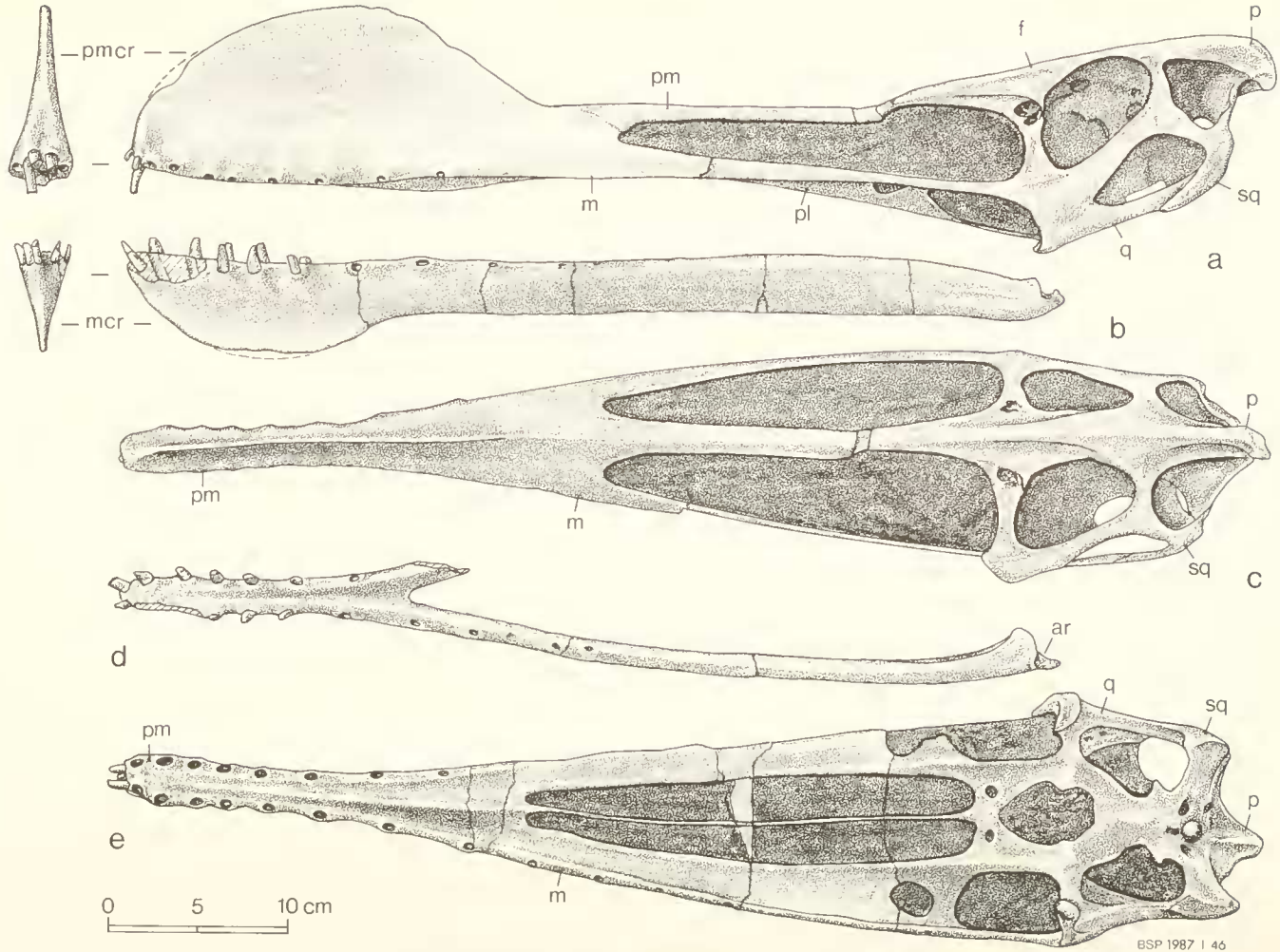
The most striking feature of the skull is a large, sagittal, premaxillary crest on top of the snout. In contrast to the bony crest in *Anhanguera blittersdorffi*, this crest is developed at the distal end leaving no pointed upper jaw in front as in *Anhanguera*. Also it is rather high with a fairly steep front margin. Just above the front teeth there is a triangular flat area with a shallow medial depression. A similar depression is present at the front end of the upper jaw of *Criorhynchus simus* (see fig. 4a). The premaxillary crest decreases continually from the lateral margins of the jaw to the top forming a thin bony blade only a few millimeters thick. The crest occupies about 27% of the total length of the skull.

The pattern of the skull fenestration is similar as in *Anhanguera* decribed by Campos & Kellner (1985) (see. fig. 1). A splint-like process of the lachrymal is not projecting into the orbit as in that genus, however. The quadrate is rather flat and not as steep as in *Araripesaurus* (see fig. 1). The parietal forms a masive, short and blunt crest overhanging the posterior margin of the skull. It is expanded posteriorly. Probably, it provided areas for the origin of jaw muscles.

The palate shows very long internal nares medially divided by a thin rod-like vomer, and framed by the palatines and the pterygoids. There are almost circular postpalatinal openings and square subtemporal fenestrae separated by the ectopterygoids. The margins of a large interpterygoid vacuity are formed by the pterygoids and the basisphenoid. The quadrate is firmly fused with the pterygoid and the basisphenoid, a condition met with in the skull of *Santanadactylus*, but different from the condition in *Araripesaurus* (see Wellnhofer 1985). In general, all skull bones show a high degree of coossification, so that only a few sutures can be distinguished.

Anterior to the internal nares the palate is elevated to a high medial ridge fitting into a corresponding deep groove on the mandibular symphysis. To the front end the upper jaw narrows down to a minimum of 25 mm width increasing only a little anteriorly.

There are 13 teeth in each side of the upper jaw. Distinction between premaxillary and maxillary teeth is not possible, however. Only three front teeth are preserved but their points being broken off. In cross section they are circular and smaller than the following teeth as far as can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be estimated from the sizes of the alveoli. The diameter of the front teeth at the margin of the alveoli is 5,8 mm, whereas the diameter of the following alveoli measures eight to nine mm. Only the anterior seven teeth are strong, the posterior five must have been small and short. Except for the two front teeth which were directed slightly forward, their position was upright. The upper dentition consists of only half the number of teeth as in *Anhanguera*.

The occiput shows the principal characters as described in *Araripesaurus* by WELLNHOFER (1985: 153), but it appears to be much wider in *Tropeognathus*. The parasphenoid/basisphenoid forms a large bony plate as is the case with the fused exoccipital/opisthotic (= otoccipital). The occipital condyle is situated rather high on the occiput and directed posterioventrally. Its diameters are 11,8 and 10 mm. It is slightly depressed dorsally. The circular foramen magnum above it has a diameter of 7 mm. The supraoccipital is triangular in outline and vaulted over the occiput. It is subdivided medially by a pronounced ridge, and provided large areas for the attachment of strong neck muscles.

Mandible: The lower jaw could be prepared out of the matrix completely. The right mandibular ramus was missing, however. A similar but smaller sagittal crest is developed ventrally on the symphysis, opposite the premaxillary crest. It is an outgrowth of the dentary and narrows down continuously to form a bony blade only a few millimeters thick. The dentaries are slender joining in a narrow symphysis almost one third the jaw length. Anteriorly, the jaw is not spoon-like expanded as in *Brasileodactylus* (see fig. 1) or in *Tropeognathus robustus* (see fig. 3). Dorsally there is a deep groove for the reception of the sagittal keel of the palate. There are 11 teeth in each dentary, the anterior six pairs being partly preserved. The first two are directed anteriorly, the following ones have an upright lateral position. All but the three posterior teeth were relatively large and strong. The retroarticular process is not preserved. The articular and surangular are greatly expanded to form a fairly narrow cylindrical socket for the articular condyle of the quadrate. Medially a deep adductor fossa is present.

Measurements (in mm):

Skull:

Total length	630
Width over the quadrates	137
Minimal width of the snout	25
Maximal height of premaxillary crest	105
Length of premaxillary crest	230

Mandible:

Length as preserved	520
Total length, estimated	540
Width of symphysis	23
Depth of mandibular crest	51
Length of mandibular crest	126

Based on the dimensions of the skull the wing span of this individual can be calculated to have been about six meters.

Fig. 2: *Tropeognathus mesembrinus* nov. gen., nov. sp., Santana Formation, Aptian, Chapada do Araripe. Holotype, BSP 1987 I 46. – a, b: Skull and lower jaw as preserved in lateral aspect with the front views of the premaxillary and mandibular crests. – c, d: Skull and lower jaw in dorsal view. – e: Skull in palatal aspect. Abbreviations: ar articular, f frontal, m maxilla, mcr mandibular crest, p parietal, pl palatine, pm premaxilla, pmcr premaxillary crest, q quadrate.

Tropeognathus robustus nov. gen., nov. sp.
Fig. 3

Holotype: BSP 1987 I 47, Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich, lower jaw.

Horizon and locality: Same as for *Tropeognathus mesembrinus*.

Etymology: robustus (Latin), for the robust appearance of the jaw.

Diagnosis: *Tropeognathus* with a deep mandibular crest. Front margin straight, forming an angle of about 50° with the upper edge of the lower jaw. In dorsal view anterior end of jaw expanded spoon-like. Strong, and in the front long teeth.

Description

The mandible was imbedded in a large nodule. The right ramus and the anterior part of the symphysis could be exposed, the left ramus is still within the nodule except for the articular region. Six front teeth are preserved in their natural position, one large tooth is displaced and lies in front of the tip of the jaw.

The typical character is again a mandibular crest, extending in a sagittal plane from the front end of the mandible ventrally. It is deeper than in *Tropeognathus mesembrinus*, and its front margin is straight, and forms an angle of about 50° with the upper edge of the jaw. Anteriorly and in dorsal view the dentary is expanded into a spoon-like shape to give enough space for the implantation of the six anteriormost large teeth which are directed anteriolaterally, and due to their curvature form a perfect tool for grasping fish. There were 17 teeth on each side, widely spaced and reaching 65% of the total length of the lower jaw. The second tooth is the longest, about 33 mm above the alveolar margin. Behind the fourth tooth there is a wider diastema, the fifth being only small. According to the size of the alveoli three large teeth followed equally spaced, and then nine smaller ones, and wider spaced. The alveoli are all laterally oriented.

The articular region is not as expanded as in *Tropeognathus mesembrinus*. The articular surface shows the characteristic oblique ridge as described by Wellnhofer (1980) which allowed the mandibular rami to spread when the jaws were opened widely. The articular is perforated by a pneumatic foramen behind the articular facets. The retroarticular process is relatively long and directed posterioventrally indicating the possibility of a wide opening of the jaws.

Measurements (in mm):

Total length of mandible	560
Maximal width of symphysis	33
Minimal width of symphysis	17
Depth of the mandibular crest	76
Length of the mandibular crest	145

Based on the dimensions of the lower jaw the wing span of this individual can be calculated as about 6,20 meters. This would be the largest pterosaur from the Santana Formation hitherto discovered.

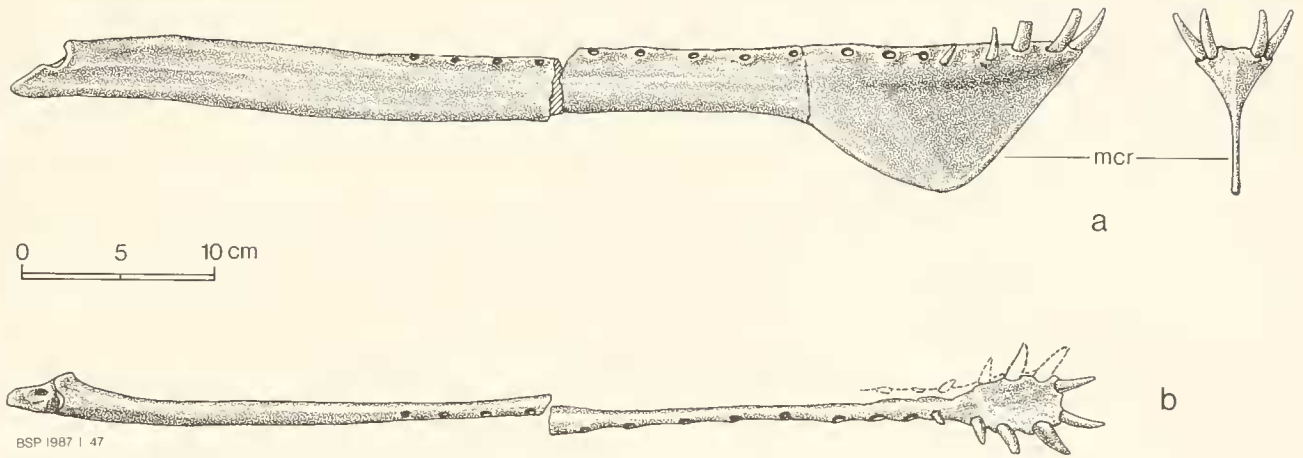

Fig. 3: *Tropeognathus robustus* nov. gen., nov. sp., Santana Formation, Aptian, Chapada do Araripe. Holotype, BSP 1987 I 47. – a: Lower jaw as preserved in right lateral view and from the front showing the mandibular crest (mcr). – b: Same jaw in dorsal aspect. The left ramus of the mandible is still enclosed within the concretion.

With regard to the peculiar premaxillary and mandibular crests of *Tropeognathus* one wonders whether those crested forms might have been known already in the last century but not recognized as such. OWEN described several jaw fragments of pterosaurs from the Wealden, the Cambridge Greensand, and the Chalk of England where different crests were developed, for example *Ornithocheirus cuvieri* and *Ornithocheirus giganteus* from the Chalk of Burham, Kent (OWEN 1851: pl. 28 and 31), and *Ornithocheirus sedgwicki* from the Cambridge Greensand (OWEN 1859: pl. 1). Of special interest here are fragments of upper jaws, described as *Coloborhynchus clavirostris* from the Wealden of Hastings (OWEN 1874: pl. 1) and *Criorhynchus simus* from the Cambridge Greensand (OWEN 1861: pl. 1; fig. 4a, this paper). Both have been synonymized by WELLNHOFER (1978) and placed in a separate family, Criorhynchidae.

Only the fragmentary front ends of the upper jaws are preserved in these two specimens, nevertheless indicating the presence of a strong premaxillary crest at the very tip of the snout as in *Tropeognathus* from Brazil. There is also a slight, shallow depression at the front end of the crest as well as a strong dentition.

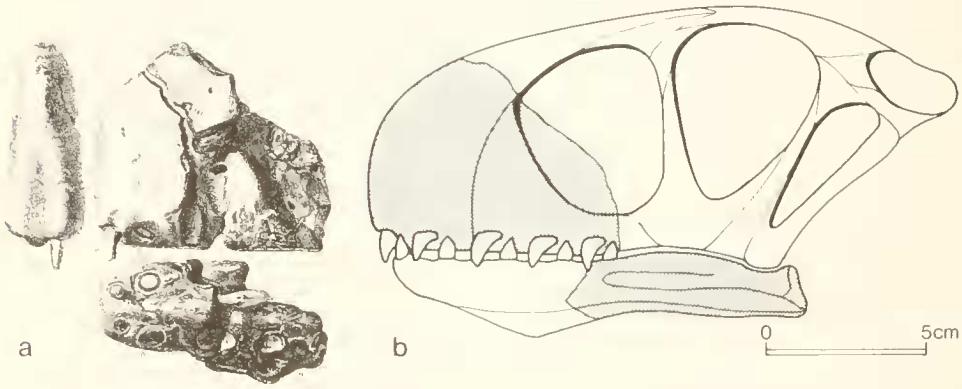

Fig. 4: *Criorhynchus simus* (OWEN), Cambridge Greensand, Cenomanian, Cambridge, England. – a: Front end of upper jaw, holotype, original illustration after OWEN (1861, T. 1, Fig. 1, 3, 5). – b: Restoration of the skull based on this jaw fragment and the posterior part of a mandible after ARTHABER (1919). This restoration is considered here to be wrong. Size and shape of the jaw fragment suggest a similar premaxillary crest as developed in *Tropeognathus* from Brazil. Therefore, *Criorhynchus* must have had a much longer skull.

It has always been a puzzle, how *Criorhynchus* might have looked like. In 1919, ARTHABER made an attempt to restore the skull of *Criorhynchus* using the fragments of the premaxillary and of the lower jaw originally assigned to the same species by OWEN (1861: pl. 1, figs. 1–10). ARTHABERS restoration resulted in a rather short and high skull (fig. 4b) which remained doubtful and highly speculative, however, compared with the very fragmentary remains it was based on.

But now, after the complete skulls and mandibles of these Brazilian pterosaurs with premaxillary and mandibular crests are known, it is – in my opinion – fairly clear that the high upper jaw of *Criorhynchus* was in fact developed as a premaxillary crest forming the front end of a larger and longer skull similar to *Tropeognathus*. This – in turn – suggests the inclusion of the

new Brazilian genus in the family Criorhynhidae which is supported also by the similar dentitions of *Criorhynchus* and *Tropeognathus*.[1])

In general, there is much more similarity between the Brazilian and the English Cretaceous pterosaurs than hitherto realized. This is supported by similar or identical morphological characters in the skull (crests, palate, dentition) as well as in the postcranial skeleton (vertebrae, carpals, humeri etc.) of the Brazilian *Araripesaurus, Santanadactylus,* and yet undescribed material, and of the different English species of *Criorhynchus* and *Ornithocheirus*. Considering the palaeogeographical situation during the Lower Cretaceous, and the high mobility of large flying vertebrates, as they were, the wide palaeobiogeographical distribution of the Criorhynchidae and the Ornithocheiridae can be easily explained.

Finally, the new genus *Tropeognathus* should be an example that the more complete pterosaurs from the Brazilian Santana Formation could help to understand the rather fragmentary pterosaurian remains of the English Cretaceous much better.

Function of the Crests

Pterodactyloid pterosaurs with bony crest-like structures on the skull are not unusual. The most common example is *Pteranodon* with a long parietal crest of different shape in different species. But also in *Dsungaripterus* and *Gallodactylus* parietal crests are developed, although much smaller. As mentioned above (p. 184), ornithocheirids and criorhynchids of the English Cretaceous seem to have had cranial and mandibular crests of different size and shape, too. Sagittal crests on the premaxilla are present in *Dsungaripterus, Germanodactylus, Gnathosaurus* (Wellnhofer 1978), *Ctenochasma* (Buisonje 1981) and *Anhanguera* (Campos & Kellner 1985).

Certainly, these different crests must have had different functions, for example as aerodynamic rudders or as areas for muscle attachment. In *Tropeognathus* large sagittal crests could be found at the front end of the jaws, for the first time. Clearly, they could not have served as areas for the attachment of jaw musculature, nor were they of particular use as aerodynamic stabilizers. As well as the beak, these crests must have been covered by horny sheaths which made them smooth and even larger.

In my opinion, the advantage of terminal crests would have been that they functioned like the keel of a boat, stabilizing the jaws in the water. With good reason we can suppose that these large pterosaurs were fish-eaters. When catching fish the tips of the jaws were submerged skimming the water with high speed. Due to the keel-like shape of the crests flow resistance was reduced, and the large head remained stabil in this situation. The terminal jaw crests of *Tropeognathus* could thus be viewed as hydrodynamic rather than aerodynamic stabilizers.

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[1]) De Buisonje (1980) assigned also the genus *Santanadactylus* to the Criorhynchidae. For comments on this see Wellnhofer (1985: 129).

I wish to thank also Ernst Schmieja, senior preparator of the Bavarian State Collection, who carried out all the preparations. Without his enthusiasm, his patience, and his professional skill this scientific study would not have been possible. I also thank Franz Höck, University Institute of Palaeontology and Historical Geology, Munich, for the photographs he took of the specimens. I used them as basis for the drawings.

Finally I wish to thank Dr. Angela Milner who made pterosaur material of the British Museum of Natural History in London available for comparative studies, and David Unwin, Reading University, for valuable discussions.

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